OSTEOLOGY OF GALLINACEOUS BIRDS

J. Alan Holman

The order Galliformes comprises a large group of almost worldwide distribution, yet its families are quite similar in basic morphology, and interfamilial hybrids occur. These factors have made a natural classification difficult, and at the present time several systems are in use.

The classification generally followed in the United States is that of Wetmore (1960). He divides the order Galliformes into two suborders, the Opisthocomi which includes the hoatzins of the family Opisthocomidae, and the suborder Galli for the remaining groups. The suborder Galli is divided into two superfamilies, the Cracoidea, and the Phasianoidea. The superfamily Cracoidea includes the families Megapodiidae (mound-builders), and Cracidae (curassows). The superfamily Phasianoidea includes the families Tetraonidae (grouse), Phasianidae (pheasants, quails, peacocks), Numididae (guineafowl), and Meleagrididae (turkeys).

Ridgway and Friedmann (1946) follow the classification of Wetmore, but further divide the Phasianidae into three subfamilies, the Odontophorinae (New World quails), Perdicinae (Old World quails), and Phasianinae (pheasants, junglefowls, peacocks).

Other interpretations are given by Stresemann (1959), who treats the Galli and Opisthocomi of Wetmore as separate orders; and by Sibley (1960), who considers the order Galliformes to be composed of three families, the Megapodiidae, the Phasianidae (with subfamilies Phasianinae, Meleagridinae, Numidinae, Tetraoninae, and Cracinae), and the Opisthocomidae.

Mayr and Amadon (1951) consider the order Galli (Galliformes of Wetmore) to be composed of five families, Megapodiidae, Cracidae, Phasianidae (with subfamilies Phasianinae, Numidinae, and Tetraoninae), Meleagrididae, and Opisthocomidae.

Brodkorb (1964) recognizes no suborders or superfamilies in the Galliformes and recognizes five families, Cracidae (with living subfamilies Cracinae and Penelopinae), Opisthocomidae, Megapodiidae, Numididae, and Phasianidae (with subfamilies Odontophorinae, Phasianinae, Tetraoninae, and Meleagrinae).

Several recent studies utilizing new fossil material or employ-

ing new approaches and techniques have attempted to evaluate the relationships among the Galliformes. These include papers by Tordoff and Macdonald (1957), early Oligocene fossils; Taibel (1961), physio-ethological characters; Hudson, Lanzollotti, and Edwards (1959), pelvic limb musculature; Sibley (1960), egg-white protein electrophoresis; and Mainardi (1960, 1963), Mainardi and Guerra (1959), and Mainardi and Taibel (1962 a and b), immunological studies.

During a recently published study of postcranial osteology of fossil and living New World quails (Holman, 1961), skeletons of representatives of the families of galliform birds were examined in order to ascertain the status of the New World quails. It then became evident that in many cases the relationships between gallinaceous groups were reflected by the postcranial skeleton. With the study of additional material, the present paper has grown out of the earlier work.

The classification of Wetmore as modified by Ridgway and Friedmann will be followed in the present paper through the sections on comparative osteology and evolutionary trends.

Acknowledgments

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William Quinn of Illinois State University made the drawings.

Materials and Methods

The skeletal collection of Pierce Brodkorb at the University of Florida and that of Robert D. Weigel at Illinois State University were supplemented by material borrowed from the United States National Museum (through Herbert Friedmann), University of California Museum of Vertebrate Zoology (through Frank A. Pitelka), University of Michigan Museum of Zoology (through H. B. Tordoff), University of Kansas Museum of Natural History (through Richard F. Johnston), and Southern Illinois University Wildlife Research Collection (through W. D. Klimstra).

The number of specimens studied is listed below, with incomplete skeletons given in parentheses.

Megapodiidae: *Alectura lathami* 1, *Leipoa ocellata* 1, *Macrocephalon maleo* 1, *Megapodius freycinet* 1.

Cracidae: *Crax globulosa* 1, *C. rubra* 1, *Mitu mitu* 1, *Ortalis vetula* (4), *Penelopina nigra* (1).

Tetraonidae: *Bonasa umbellus* 6 (1), *Canachites canadensis* 1 (2), *Centrocercus urophasianus* 4 (1), *Dendragapus fuliginosus* (1), *D. obscurus* 3 (1), *Lagopus lagopus* 4, *L. leucurus* 1, *L. mutus* 2, *Lyrurus tetrix* 1 (3), *Tetrao parvirostris* 1, *Tympanuchus cupido* 3 (1), *T. pallidicinctus* 2 (2), *Pedioecetes phasianellus* 2.

Numididae: *Acryllium vulturinum* 7, *Numida meleagris* 2.

Meleagrididae: *Meleagris gallopavo* 8.

Phasianidae, Phasianinae: *Argusianus argus* 1, *Catreus wallichii* 1, *Chrysolophus pictus* 1, *Gallus gallus* 3, *Gennaeus nycthemerus* 1, *Lophophorus impejanus* 1, *Pavo cristatus* 1, *P. muticus* 2, *Phasianus colchicus* 3.

Phasianidae, Perdicinae: *Alectoris graeca* 2, *A. rufa, Coturnix coturnix* 3 (1), *Francolinus bicalcaratus* (1), *Perdix perdix* 1 (1).

Phasianidae, Odontophorinae: *Callipepla squamata* 4, *Colinus leucopogon* 4, *C. nigrogularis* (2), *C. virginianus* 99 (5), *Cyrtonyx montezumae* 3, *Dactylortyx thoracicus* 3, *Dendrortyx leucophrys* 1, *Lophortyx californica* 2 (1), *L. douglasii* 2, *L. gambelii* 2, *Odontophorus gujanensis* 1 (1), *O. guttatus* 1, *O. stellatus* 1, *Oreortyx picta* 4, *Philortyx fasciatus* 1, *Rhynchortyx cinctus* 1.

Opisthocomidae: *Opisthocomus hoazin* 2.

Anatomical nomenclature in this paper follows that of Howard (1929).

Comparative Osteology

Characters found useful in the definition of galliform groups and those showing interrelationships are presented in this section. With one exception these are qualitative characters. A large number of intermembral proportions were taken (many of these are included in the doctoral dissertation of J. Alan Holman at the University of Florida Library, 1961), but most of these were of no value in the definition of group relationships. The skeletal elements discussed are those most frequently found as fossils and with one exception are postcranial. Statements made in this section are based only on the specimens listed above.

Rostrum (Plate 3)

Long, deep, strongly decurved (Cracidae); short, deep, strongly decurved (Odontophorinae); long, shallow, slightly to moderately decurved (other Galliformes).

Dorsal bony knob present (*Mitu, Crax* of Cracidae); bony knob absent (other Galliformes).

Nasal fossae reduced (Opisthocomidae); fossae large (other Galliformes).

Process of nasal bone projecting anteriorly from middle of posterior margin of nasal fossae (*Macrocephalon* of Megapodiidae; Opisthocomidae); without this condition (other Galliformes).

Sternum (Plate 1)

Manubrial spine ankylosed to furculum (Opisthocomidae); manubrial spine free anteriorly (other Galliformes). Manubrial spine with very large dorsal foramen (Cracidae); spine with moderately large dorsal foramen (*Catreus, Phasianus, Argusianus* of Phasianinae; Numididae); spine with slight pneumatic perforations dorsally (some *Tympanuchus cupido, Lagopus mutus, Lyrurus tetrix, Bonasa umbellus* of Tetraonidae); spine with obsolete dorsal foramen (some *Pedioecetes* of Tetraonidae); spine without dorsal foramina (other Galliformes).

Anterior lateral processes absent (Opisthocomidae); anterior lateral processes present, short, broad, at right angle to long axis of sternum (Megapodiidae; Cracidae); anterior lateral processes present, short, broad, at about 45 degree angle to long axis of sternum (Numididae); anterior lateral processes present, moderately short and wide, nearly parallel to long axis of sternum (*Tetrao parvirostris* of Tetraonidae; *Pavo* of Phasianinae); anterior lateral processes present, elongate and slender, nearly parallel to long axis of sternum (other Galliformes).

Anterior sternal plate highly pneumatic (Megapodiidae; Cracidae; Opisthocomidae); plate moderately pneumatic (Numididae; Meleagrididae); plate moderately or slightly pneumatic (Tetraonidae; Phasianinae); plate moderately, slightly or non-pneumatic (Odontophorinae); plate slightly or non-pneumatic (Perdicinae).

Sternum with only one pair of short notches (Opisthocomidae); sternum with two pairs of notches (other Galliformes). Inner sternal notches short, thus posterior lateral and posterior medial proc-

Plate 1. Sternum of Galliformes. A, *Crax globulosa*; B, *Acryllium vulturinum*; C, *Phasianus colchicus*; D, *Opisthocomus hoazin*.

esses arising independently from sternum (Megapodiidae; Cracidae); inner sternal notches longer, thus posterior lateral and posterior medial processes arising from common base (other Galliformes).

Carina reduced in extent, but swollen, apex directed ventrally, posterior face excavated as elliptical concavity, without anterolateral extending ridges (Opisthocomidae); carina well developed, narrow throughout, apex rotated anteriorly, without elliptical concavity, with anterolateral extending ridges (other Galliformes).

Coracoid (Plate 3)

Medial surface of head fused to furculum (Opisthocomidae); medial surface of head not fused to furculum, flattened (Meleagrididae) or rounded (other Galliformes).

Brachial tuberosity fused to furculum (Opisthocomidae); tuberosity not fused to furculum, without overhanging ventral portion (Megapodiidae; Cracidae; Meleagrididae) or with overhanging ventral portion (other Galliformes).

Dorsal intermuscular line not raised distally (Megapodiidae; Cracidae; most Phasianinae; Meleagrididae); line slightly raised distally (*Gallus, Chrysolophus* of Phasianinae; Numididae); line slightly or sharply raised distally (Tetraonidae); line sharply raised distally (Odontophorinae; Perdicinae; Opisthocomidae).

Distal dorsal face without pneumatic fossa (most Megapodiidae; Odontophorinae; Perdicinae; Numididae); face with large pneumatic fossa (*Leipoa* of Megapodiidae; other Galliformes).

Sterno-coracoidal process without terminal knob (*Leipoa* of Megapodiidae; Cracidae; *Dendrortyx* of Odontophorinae; Opisthocomidae); process ending in obsolete terminal knob (*Philortyx* of Odontophorinae; Phasianinae; Numididae; Meleagrididae); process ending in well developed terminal knob (other Galliformes).

Scapula (Plate 2)

Ventral base of glenoid facet with large pneumatic fossa (most Megapodiidae; Cracidae); facet with small pneumatic fossa (*Argusianus* of Phasianinae; some Opisthocomidae); facet without pneumatic fossa (*Megapodius* of Megapodiidae; other Galliformes).

Area mediad to glenoid facet in dorsal aspect with depression (Odontophorinae; Perdicinae); area with slight depression (*Mega-*

podius of Megapodiidae; *Crax* of Cracidae; *Lophophorus, Phasianus, Chrysolophus* of Phasianinae; *Acryllium* of Numididae); area without depression (other Galliformes).

Bridge between acromion process and glenoid facet with distinct pneumatic fossa (Tetraonidae; *Pavo* of Phasianinae); bridge moderately pneumatic (Opisthocomidae); bridge slightly pneumatic (*Argusianus* of Phasianinae); bridge non-pneumatic (other Galliformes).

Acromion process straight (*Leipoa* of Cracidae; Tetraonidae; Meleagrididae; Opisthocomidae); process deflected (other Galliformes).

Dorsal base of shaft with pneumatic fossa (Meleagrididae); base non-pneumatic (other Galliformes).

Blade very elongate (Odontophorinae; *Coturnix* of Perdicinae); blade moderately elongate (*Alectoris, Perdix* of Perdicinae); blade moderately short and wide (*Megapodius, Leipoa* of Megapodiidae; *Ortalis* of Cracidae; Tetraonidae; most Phasianinae); blade very short and wide (*Alectura, Macrocephalon* of Megapodiidae; *Pavo* of Phasianinae; other Galliformes). Apex of blade without terminal expansion (*Alectura, Macrocephalon* of Megapodiidae; Cracidae; *Pavo* of Phasianinae; *Acryllium* of Numididae; Opisthocomidae); apex terminally expanded (other Galliformes).

Humerus (Plate 2)

Pneumatic fossa very small (Megapodiidae; Cracidae; Opisthocomidae); fossa small, but somewhat larger than in preceeding groups (Numididae; Meleagrididae); fossa moderately enlarged (Tetraonidae; *Perdix* of Perdicinae; Phasianinae); fossa much enlarged (Odontophorinae; most Perdicinae).

Internal anconal border of bicipital crest narrow (Odontophorinae; most Perdicinae); border very wide (Megapodiidae); border moderately wide (*Perdix* of Perdicinae; other Galliformes).

With inner shelf extending from medial bar to internal bicipital surface absent (most Odontophorinae, *Alectoris, Coturnix* of Perdicinae); inner shelf present, but incomplete (*Megapodius* of Megapodiidae; Tetraonidae; *Odontophorus gujanensis* of Odontophorinae; Opisthocomidae); inner shelf present, complete (other Galliformes).

Fossa II (Ashley, 1941) absent (Megapodiidae; Cracidae; Opis-

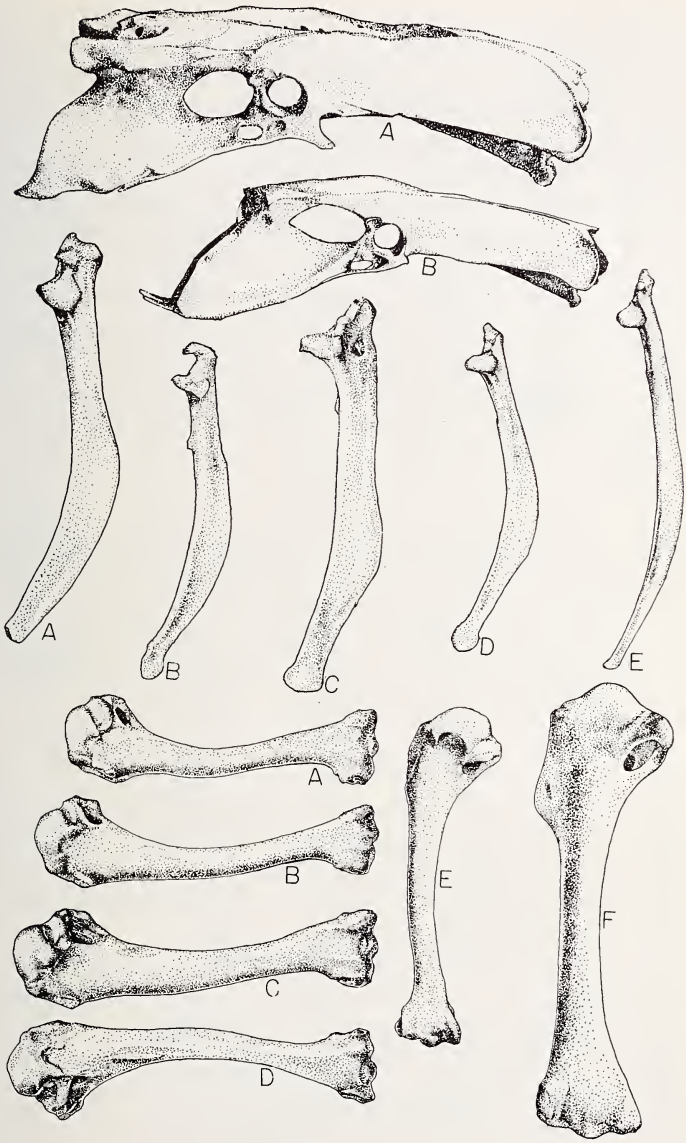


Plate 2. Osteology of Galliformes. Upper row: Pelvis of A, *Phasianus colchicus*; B, *Colinus virginianus*.

Middle row: Dorsal view of scapula of A, *Mitu mitu*; B, *Numida meleagris*; C, *Meleagris gallopavo*; D, *Phasianus colchicus*; E, *Colinus virginianus*.

Lower row: Anconal view of humerus of A, *Crax globulosa*; B, *Numida meleagris*; C, *Meleagris gallopavo*; D, *Phasianus colchicus*; E, *Colinus virginianus*; F, *Opisthocomus hoazin*.

thocomidae); fossa II well developed (most Odontophorinae; *Coturnix* of Perdicinae); fossa II very weakly developed (*Dendrortyx* and *Odontophorus* of Odontophorinae; other Galliformes).

Bicipital crest with lateral margin truncated (*Alectura* of Megapodiidae; *Mitu* of Cracidae; Numididae; Opisthocomidae); margin rounded (other Galliformes).

Median crest very strongly developed, knoblike (Opisthocomidae); crest only moderately developed, flattened (other Galliformes).

Deltoid crest low on shaft, apex well below level of pneumatic fossa and bicipital crest, rotated anconally so that apex visible in anconal view (Opisthocomidae); crest high on shaft, apex at level of middle of pneumatic fossa and bicipital crest, rotated palmarly so that apex not visible in anconal view (other Galliformes).

Ulna

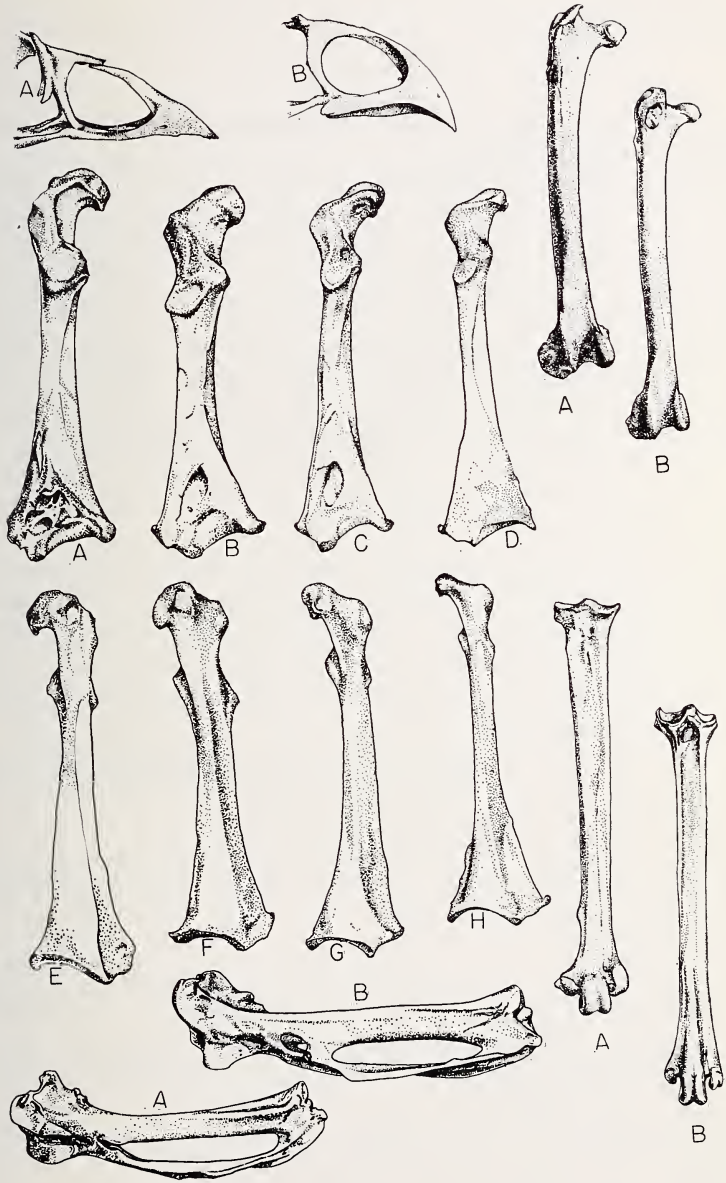
External cotyla weakly developed (Meleagrididae); cotyla moderately developed (*Acryllium* of Numididae); cotyla well developed (other Galliformes). Margin of external cotyla flattened (*Alectura* of Megapodiidae; *Crax globulosa* of Cracidae; *Dendrortyx, Odontophorus guttatus* of Odontophorinae; *Argusianus* of Phasianinae; Meleagrididae); margin rounded (other Galliformes).

Carpometacarpus (Plate 3)

Pisiform process at level of ligamental attachment (most Megapodiidae; Cracidae; Tetraonidae; most Perdicinae; *Acryllium* of Numididae; some Opisthocomidae); process produced beyond level of ligamental attachment (*Alectura* of Megapodiidae; *Coturnix* of Perdicinae; other Galliformes).

Intermetacarpal process absent (most Megapodiidae; Numididae, Opisthocomidae); process represented by a minute point (*Alectura* of Megapodiidae; Cracidae; *Pavo* of Phasianinae); process weakly developed, not extending to level of metacarpal III (some individuals of *Crytonyx* of Odontophorinae; *Coturnix* of *Perdicinae; Gennaeus, Catreus* of Phasianinae); process well developed, extending to metacarpal III (other Galliformes).

Carpal trochlea with external rim continuing distad beyond ligamental notch (Megapodiidae; Cracidae; Opisthocomidae); with external rim ending at ligamental notch (other Galliformes).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Metacarpal III about as wide as metacarpal II (Opisthocomidae); III much narrower than II (other Galliformes).

Pelvis (Plate 2)

Pelvis very wide and shallow (Tetraonidae); relatively narrow and deep (other Galliformes).

Pectineal process represented by only a minute point (Megapodiindae; Opisthocomidae); process well developed, long and narrow (Perdicinae; most Phasianinae); process small, short (*Pavo cristatus* of Phasianinae; other Galliformes). Pectineal process with pneumatic foramen on anterior border (*Leipoa, Alectura* of Megapodiidae; Cracidae); process without pneumatic foramina (*Megapodius, Macrocephalon* of Megapodiidae; most Odontophorinae; Perdicinae; Numididae); process with foramen or foramina on medial face (*Dendrortyx* of Odontophorinae; other Galliformes).

Entire renal depression highly pneumatic (most Megapodiidae); depression with a moderate number of pneumatic foramina (*Megapodius* of Megapodiidae); anterior renal depression with large pneumatic fossa (Cracidae *Acryllium* of Numididae); anterior depression with moderately large pneumatic fossa (*Numida* of Numididae); anterior renal depression with a few small pneumatic foramina (*Bonasa* of Tetraonidae; *Lophophorus, Gallus, Catreus, Argusianus, Pavo* of Phasianinae); renal depression non-pneumatic (other Galliformes).

Renal bar slender (*Ortalis* of Cracidae; *Dendrortyx, Philortyx, Oreortyx, Callipepla, Colinus, Lophortyx* of Odontophorinae; *Coturnix* of Perdicinae); bar broad (other Galliformes).

Roof formed by dorsal extensions of preacetabular ilia over synsacral vertebrae present (Opisthocomidae); preacetabular ilial roof absent (other Galliformes).

Plate 3. Osteology of Galliformes. Upper left: Rostrum of A, *Coturnix coturnix;* B, *Colinus virginianus.*

Second and third rows: Dorsal and ventral views of coracoid of A and E, *Crax globulosa;* B and F, *Meleagris gallopavo;* C and G, *Phasianus colchicus;* D and H, *Colinus virginianus.*

Bottom row: External view of carpometacarpus of A, *Crax globulosa;* B, *Meleagris gallopavo.*

Upper right: Anterior view of femur of A, *Crax globulosa;* B, *Phasianus colchicus.*

Lower right: Anterior view of tarsometatarsus of A, *Crax globulosa;* B, *Phasianus colchicus.*

Femur (Plate 3)

Head flattened, dorsal border at level of iliac facet (Meleagrididae); head swollen, dorsal border above level of iliac facet (other Galliformes).

Dorsal crest of trochanter very high (Megapodiidae; some Meleagrididae); crest low (Cracidae; *Rhynchortyx, Cyrtonyx, Odontophorus, Colinus* of Odontophorinae; Opisthocomidae); crest moderately high (other Galliformes).

Area mediad to anterior border of trochanter with pneumatic fossa (*Alectura, Leipoa* of Megapodiidae; Tetraonidae; most Phasianinae); area laterad to posterior aspect of head with pneumatic fossa (*Argusianus* of Phasianinae); both areas non-pneumatic (*Lophophorus, Gallus* of Phasianinae; other Galliformes).

Round ligament attachment deeply excavated (Opisthocomidae); attachment shallow (other Galliformes).

Tibiotarsus

Inner cnemial crest usually arising from shaft well above level of outer cnemial crest (Meleagrididae); inner cnemial crest arising at level of outer cnemial crest (most Perdicinae; *Numida* of Numididae); inner cnemial crest arising from shaft well below level of outer cnemial crest (*Coturnix* of Perdicinae; other Galliformes).

Outer cnemial crest weakly developed (Opisthocomidae); outer crest strongly developed (other Galliformes).

Tarsometatarsus (Plate 3)

Hypotarsus with two roofed calcaneal canals (*Lagopus lagopus* 1 of 4, *Bonasa umbellus* 2 of 7, *Pedioecetes phasianellus* 1 of 2, *Tympanuchus cupido* 2 of 4 of Tetraonidae; most Odontophorinae); hypotarsus with one roofed calcaneal canal (*Dendrortyx, Rhynchortyx,* most *Oreortyx* of Odontophorinae; other Galliformes).

Inner calcaneal ridge with distal extension running about one-third to three-fourths the way down shaft (most Tetraonidae; *Alectoris* of Perdicinae; most Phasianinae; Meleagrididae); ridge without distal extension (*Lagopus lagopus* 2 of 4, *Bonasa umbellus* 4 of 7, *Centrocercus urophasianus* 2 of 5 of Tetraonidae; *Gallus* of Phasianinae; other Galliformes).

Posterior shaft with spur core in male (Phasianinae; Meleagrididae); posterior shaft with rudimentary spur core in male (*Alectoris* of Perdicinae); posterior shaft without spur core (other Galliformes).

Trochleae short, metacarpal III only slightly extending below level of metacarpals II and IV (Opisthocomidae); trochleae moderately long, metacarpal III extending well below level of metacarpals II and IV (other Galliformes).

Trochlea for digit II at level of trochlea for digit IV (*Megapodius, Macrocephalon* of Megapodiidae; Cracidae; Opisthocomidae); II slightly elevated above IV (*Leipoa, Alectura* of Megapodiidae); II well above IV (other Galliformes).

Intermembral Proportions

Pelvis longer than sternum (Megapodiidae; Opisthocomidae); pelvis shorter than sternum (other Galliformes).

EVOLUTIONARY TRENDS

Most authors have considered the superfamily Cracoidea to represent the most primitive of the gallinaceous birds. The recent work of Hudson, Lanzillotti, and Edwards (1959) on the pelvic limb musculature in galliform birds tends to confirm this view. Moreover, Mainardi and Taibel (1962b) go so far as to state there is evidence that all galliform birds have descended from an ancestral stock similar to the family Cracidae. These remarks are based on morphological and paleontological data. If indeed this family represents the most primitive living galliform group, then several trends in other galliform taxa toward modification of structures found in the Cracidae become evident. These trends are summarized below.

Sternum

(1) *Increased excavation of sternum by notches.* Cracidae, Megapodiidae, Opisthocomidae: sternum excavated by one or two pairs of short notches. Other Galliformes: sternum excavated by two pairs of long notches.

(2) *Reduction and loss of the dorsal foramen in the manubrial spine.* Cracidae: foramen very large. Numididae: foramen moderately large. Phasianinae: foramen moderately large or absent. Tetraonidae: foramen obsolete or absent. Megapodiidae, Melea-

gridídae, Perdicinae, Odontophorinae: foramen absent. In the Opisthocomidae the fusion of the manubrial spine with the furculum obscures this character.

(3) *Modification of the anterior lateral processes.* Cracidae, Megapodiidae: processes short, broad, at right angle to long axis of sternum. Numididae: processes short, broad, at 45 degree angle to long axis of sternum. Meleagrididae, Phasianinae (except *Pavo*), Perdicinae, Tetraonidae (except *Tetrao parvirostris*), Odontophorinae: processes long, narrow, parallel to long axis of sternum. In the Opisthocomidae the anterior lateral processes are missing.

(4) *Decreasing pneumaticity of the anterior sternal plate.* Opisthocomidae, Megapodiidae, Cracidae: plate highly pneumatic. Numididae, Meleagrididae: plate moderately pneumatic. Tetraonidae, Phasianinae: plate moderately or slightly pneumatic. Odontophorinae: plate moderately, slightly, or non-pneumatic. Perdicinae: plate slightly or non-pneumatic.

Coracoid

(5) *Development of an overhanging ventral portion of the brachial tuberosity.* Cracidae, Megapodiidae, Meleagrididae: overhanging ventral portion absent. Other families: overhanging ventral portion present.

(6) *Development of a sharply raised distal portion of the dorsal intermuscular line.* Cracidae, Megapodiidae, Meleagrididae: line without sharply raised distal portion. Phasianinae: line usually without sharply raised distal portion, but may be slightly raised distally. Numididae, some Tetaronidae: line slightly raised distally. Opisthocomidae, most Tetraonidae, Perdicinae, Odontophorinae: line sharply raised distally.

(7) *Loss of the large fossa on the distal dorsal face.* Opisthocomidae, Cracidae, some Megapodiidae, Meleagrididae, Phasianinae, Tetraonidae: large pneumatic fossa present. Numididae, Odontophorinae, Perdicinae, most Megapodiidae: pneumatic fossa absent.

(8) *Development of a terminal knob on the sterno-coracoidal process.* Opisthocomidae, Cracidae, *Leipoa* of Megapodiidae, *Dendrortyx* of Odontophorinae: sterno-coracoidal process without terminal knob. Numididae, Meleagrididae, Phasianinae, *Philortyx* of

Odontophorinae: terminal knob quite small. Most Megapodiidae, Perdicinae, Tetraonidae, most Odontophorinae: terminal knob well developed.

Scapula

(9) *Loss of pneumatic fossa in the ventral base of the glenoid facet.* All Megapodiidae but *Megapodius,* Cracidae: large pneumatic fossa present. Opisthocomidae, *Argusianus* of Phasianinae: small pneumatic fossa sometimes present. Other forms (pneumatic fossa absent.

(10) *General narrowing of the blade.* Opisthocomidae, Cracidae except *Ortalis,* some Megapodiidae, Numididae, Meleagrididae, *Pavo* of Phasianinae: blade very short and wide. Some Megapodiidae, *Ortalis* of Cracidae, Tetraonidae, most Phasianinae: blade moderately short and wide. Most Perdicinae: blade moderately elongate. *Perdix* of Perdicinae, Odontophorinae: blade very elongate.

(11) *Development of terminal expansion on blade apex.* Opisthocomidae, Cracidae, some Megapodiidae, *Acryllium* of Numididae, *Pavo* of Phasianinae: apex without terminal expansion. Other forms: apex terminally expanded.

Humerus

(12) *Increasing pneumaticity of the proximal end, including enlargement of the pneumatic fossa, obliteration of its inner shelf, and development of a second fossa.* Opisthocomidae, Cracidae, Megapodiidae: pneumatic fossa very small, with inner shelf extending from medial bar to internal bicipital surface; the shelf is incomplete in the Opisthocomidae and *Megapodius* of the Megapodiidae. Numididae, Meleagrididae: pneumatic fossa small, but somewhat larger than in preceeding forms; complete inner shelf present. Phasianinae, *Perdix* of Perdicinae, Tetraonidae (pneumatic fossa moderately large; inner shelf present, but incomplete in Tetraonidae), most Perdicinae; Odontophorinae: pneumatic fossa much enlarged; inner shelf absent except in *Odontophorus guttatus* of Odontophorinae.

Opisthocomidae, Cracidae, Megapodiidae: fossa II absent. Tetraonidae, Numididae, Meleagrididae, Phasianinae, *Alectoris, Perdix* of Perdicinae, *Dendrortyx, Odontophorus* of Odontophorinae: fossa II very weakly developed. *Coturnix* of Perdicinae, most Odontophorinae: fossa II well developed.

Carpometacarpus

(13) *Development of a long intermetacarpal process.* Opisthocomidae, Cracidae, Megapodiidae, Numididae, *Pavo* of Phasianinae: intermetacarpal process absent or represented by only a minute point. *Gennaeus, Catreus* of Phasianinae, *Coturnix* of Perdicinae, some individuals of *Cyrtonyx* of Odontophorinae: intermetacarpal process weakly developed. Remaining forms: intermetacarpal process well developed, extending to level of metacarpal III.

(14) *Modification of the external rim of the carpal trochlea.* Opisthocomidae, Megapodiidae, Cracidae: external rim of carpal trochlea continues distad beyond ligamental notch. Other forms: external rim of carpal trochlea ends at ligamental notch.

Pelvis

(15) *Decreasing pneumaticity of renal depression.* Some Opisthocomidae, Cracidae, Megapodiidae, Numididae: renal depression much or moderately perforated by pneumatic foramina, or with a pneumatic fossa. *Bonasa* of Tetraonidae, *Lophophorus, Gallus, Catreus Argusianus, Pavo* of Phasianinae: anterior renal depression with a few small pneumatic foramina. Other forms: renal depression non-pneumatic).

Tarsometatarsus

(16) *Elevation of the trochlea for digit II.* Opisthocomidae, Cracidae, *Megapodius, Macrocephalon* of Megapodiidae: trochlea for digit II at level of trochlea for digit IV. *Leipoa, Alectura* of Megapodiidae: trochlea for digit II slightly elevated above trochlea for digit IV. Other forms: trochlea for digit II elevated well above trochlea for digit IV.

Among the above characters the cracid-like condition is shown (at least by some genera) 14 times in the Megapodiidae, 12 times in the Opisthocomidae, five times in the Numididae, five times in the Meleagrididae, twice in the Phasianinae, once in the Tetraonidae, and never in the Perdicinae and Odontophorinae.

Discussion

In many cases the families of gallinaceous birds as outlined by Wetmore (1960) and the phasianid subfamilies as outlined by Ridgway and Friedmann (1946) are difficult to define on the basis of post-

cranial osteology. Many characters that will distinguish most genera of some groups from most genera of other groups break down in a few genera, in a single genus, or even in species and individuals. Moreover, there are few characters that are unique at the familial and subfamilial level other than in the Opisthocomidae.

Several osteological characters are shared by the families Cracidae, Megapodiidae, and Opisthocomidae. Indeed, I believe there is not much doubt that these families are much more closely related to each other than to the remaining gallinaceous birds.

Among these remaining galliform groups there seems to be a tendency for some groups to depart more radically than others from the primitive cracid-like condition.

Following is a tentative arrangement of gallinaceous families and subfamilies based on the rostrum and postcranial osteology.

Order Galliformes

Family Cracidae
Family Megapodiidae
Family Opisthocomidae
Family Numididae
Family Meleagrididae
Family Phasianidae
  Subfamily Tetraoninae
  Subfamily Phasianinae
  Subfamily Odontophorinae

Family Cracidae

The closest osteological affinities of the Cracidae are with the Megapodiidae. The following characters will separate the two families:

Sternum: less than twice as long as inner notch. Megapodiidae, more than twice as long as inner notch. Manubrial spine with very large dorsal foramen. Megapodiidae, dorsal foramen absent.

Ulna: external cotyla weakly developed. Megapodiidae, external cotyla well developed.

Femur: dorsal crest low. Megapodiidae, dorsal crest very high.

The next closest affinities of the Cracidae are with the Opisthocomidae.

Family Megapodiidae

The closest osteological affinities are with the Cracidae, but many characters are shared with the Opisthocomidae.

Family Opisthocomidae

The hoatzin appears to be at once primitive and very highly specialized. Its closest osteological affinities are with the Cracidae and Megapodiidae, but it has many unique characters as follow:

Rostrum: nasal fossae reduced. Other forms, nasal fossae large.

Sternum: manubrial spine ankylosed to furculum, sternal plate lacking anterior lateral processes, only one pair of very short notches; carina reduced in extent, but swollen, apex directed ventrally, posterior face excavated as elliptical concavity, lacking anterolateral extending carinal ridges. Other forms, manubrial spine free anteriorly; sternal plate with anterior lateral processes and two pairs of notches; carina well developed and narrow throughout, its apex directed anteriorly, elliptical concavity lacking on its posterior face, carinal ridges extending anterolaterally.

Coracoid: medial surface of head and brachial tuberosity fused to furculum. Other forms, medial surface of head and brachial tuberosity free.

Humerus: medial crest strongly developed, knoblike; deltoid crest low on shaft, its apex well below level of pneumatic fossa and bicipital crest; rotaed anconally so apex visible in anconal view. Other forms, median crest moderately developed, flattened; deltoid crest high on shaft, its apex at level of middle of pneumatic fossa and bicipital crest; rotated palmarly so apex not visible in anconal view.

Carpometacarpus: metacarpal III about as wide as metacarpal II. Other forms, metacarpal III much narrower than metacarpal II.

Pelvis: roof formed by dorsal extensions of preacetabular ilium over synsacral vertebrae present. Other forms, roof absent.

Femur: round ligament attachment much excavated. Other forms, round ligament attachment shallow.

Tibiotarsus: outer cnemial crest weakly developed. Other forms, crest strongly developed.

Tarsometatarsus: trochleae short, metacarpal III extends only slightly below metacarpals II and IV. Other forms, trochleae

longer, metacarpal III extends well below level of metacarpals II and IV.

Family Numididae

This family has some osteological characters shared by the Cracidae but it shows more similarities to other more advanced gallinaceous groups. There is one unique character as follows:

Sternum: anterior lateral processes short, broad, making angle of about 45 degrees to long axis of sternum. Other forms, anterior lateral processes when present either long and narrow and parallel to long axis of sternum, or short and broad and at right angle to long axis of sternum.

Family Meleagrididae

Although the turkeys have a few cracid-like characters, two are unique.

Scapula: dorsal base of shaft with pneumatic fossa. Other forms, dorsal base of shaft without fossa.

Femur: head flattened, its dorsal border at level of iliac facet. Other forms, head swollen, its dorsal border above level of facet.

Family Phasianidae

With the exception of the genus *Pavo,* this heterogeneous group shows more modifications from the cracid skeleton than any other gallinaceous family. There are no osteological characters unique to the Phasianidae as a whole, which thus must be defined by a combination of characters.

Subfamily Tetraoninae

The grouse appear to have closest skeletal affinities with the pheasants, junglefowls, peacocks, and Old and New World quails, and for this reason are placed as a subfamily of the Phasianidae. The very shallow and wide pelvis is a unique character of the Tetraoninae.

Subfamily Phasianinae

This subfamily includes both the Phasianinae and Perdicinae of Ridgway and Friedmann (1946). On one hand the Old World quails (Perdicinae of Ridgway and Friedmann) show some basic resemblances to the pheasants, but on the other hand some of the

same trends in modification of skeletal structures as found in the New World quails, probably through parallel evolution in the Old and New World birds.

The genus *Pavo* has certain skeletal similarities to both *Numida* and *Acryllium* of the Numididae, not shared by other birds of the subfamily Phasianinae. Some of these include the short, broad anterior lateral processes of the sternum, the lack of a well defined intermetacarpal process of the carpometacarpus, and the lack of a well developed pectineal process of the pelvis in *Pavo cristatus.* Perhaps *Pavo* is a linking genus between the Phasianinae and the Numididae. Mainardi and Taibel (1962b) state "*Pavo* is immunologically more closely related to *Numida* than to any other phasianid". They also state " . . . they hybridize easily, have quite similar karotypes, and the same modality of moult of the rectrices . . . ".

Subfamily Odontophorinae

In a previous paper (Holman, 1961) I considered the New World quails to represent a separate family, the Odontophoridae. At the present time I feel that it is best to retain the New World quails as a subfamily of the Phasianidae because of the characters that are shared with the grouse, pheasants, junglefowl, peacocks, and Old World quails.

The Odontophorinae comprise the phasianid group that departs most radically from the cracid-like skeleton, although some parallel developments have taken place in the Old World quails of the subfamily Phasianinae. Characters that separate the Odontophorinae from the Phasianinae are as follow:

In the rostrum, (1) Odontophorinae, rostrum short, deep, strongly decurved; Phasianinae, rostrum long, shallow, slightly decurved.

In the sternum, (1) Odontophorinae, manubrial spine without dorsal foramen; Phasianinae, manubrial spine often with dorsal foramen.

In the coracoid, (1) Odontophorinae, dorsal intermuscular line sharply raised distally; Phasianinae, dorsal intermuscular line usually not raised, or only slightly raised distally. (2) Odontophorinae, ventral intermuscular line terminating at tip of sterno-coracoidal process or occasionally in middle of distal border of sternal facet; Phasianinae, ventral intermuscular line often terminating near lateral end of sternal facet. (3) Odontophorinae, distal dorsal face

non-pneumatic; Phasianinae, distal dorsal face almost always with a large pneumatic fossa. (4) Odontophorinae, sterno-coracoidal process usually terminating in well developed terminal knob; Phasianinae, sterno-coracoidal process usually terminating in obsolete terminal knob.

In the scapula, (1) Odontophorinae, scapular blade very elongate, with its dorsal surface grooved throughout, and with its apex expanding terminally; Phasianinae, scapular blade with much variation in shape, but never as in Odontophorinae.

In the humerus, (1) Odontophorinae, pneumatic fossa much enlarged, with inner shelf in only one species of *Odontophorus;* Phasianinae, pneumatic fossa usually moderately large, usually with inner shelf extending from medial bar to internal bicipital surface. (2) Odontophorinae, fossa II usually well developed; Phasianinae, fossa II usually obsolete.

In the pelvis, (1) Odontophorinae, pectineal process obsolete; Phasianinae, pectineal process well developed, long (*Pavo cristatus* is the single exception with the pectineal process obsolete, whereas it is rather well developed in *Pavo muticus*). (2) Odontophorinae, renal bar non-pneumatic; Phasianinae, renal bar often with pneumatic foramen.

In the tarsometatarsus, (1) Odontophorinae, hypotarsus usually with two roofed calcaneal canals; Phasianinae, hypotarsus with one roofed calcaneal canal. (2) Odontophorinae, inner calcaneal ridge without distal extension; Phasianinae, inner calcaneal ridge usually with distal extension that runs two-thirds the way down shaft. (3) Odontophorinae, posterior shaft usually without spur core; Phasianinae, posterior shaft usually with spur core, or rudimentary spur core in male.

It is interesting to note that Sibley (1960) remarked that on the basis of electrophoretic patterns of egg-white proteins the New World quails might represent a separate subfamily.

Summary

On the basis of postcranial osteology the Cracidae (curassows), Megapodiidae (mound-builders), and Opisthocomidae (hoatzins) are much more closely related to each other than to the remaining groups of the Galliformes. These three families are considered to be primitive based on the thesis that the Cracidae comprise the

most primitive gallinaceous family. The Opisthocomidae show many skeletal specializations.

Among the remaining groups, the families Numididae (guineafowls), Meleagrididae (turkeys), and Phasianidae (with subfamilies Tetraoninae, grouse; Phasianinae, pheasants, junglefowls, peacocks, Old World quails; and Odontophorinae, New World quails) are recognized.

The Numididae and Meleagrididae retain a few primitive skeletal characters. In general, the Phasianidae are more advanced. The New World qauils (Odontophorinae) are considered to be the phasianid group that has departed most radically from the primitive cracid-like condition.

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Department of Biological Sciences, Illinois State University, Normal, Illinois.